

Increasing impacts by Antarctica's most widespread invasive plant species as result of direct competition with native vascular plants

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Abstract

Biological invasions represent significant economic and conservation challenges, though it is widely acknowledged that their impacts are often poorly documented and difficult to predict. In the Antarctic, one non-native vascular plant species is widespread and studies have shown negative impacts on native flora. Using field “common garden” experiments, we evaluate the competitive impact of the increasingly widespread invasive grass *Poa annua* on the only two native vascular species of Antarctica, the forb *Colobanthus quitensis* and the grass *Deschampsia antarctica*. We focus on interactions between these three plant species under current and a future, wetter, climate scenario, in terms of density of individuals. Our analysis demonstrates *Poa annua* has the potential to have negative impacts on the survival and growth of the native Antarctic vascular species. Under predicted future wetter conditions, *C. quitensis* communities will become more resistant to invasion, while those dominated by *D. antarctica* will become less resistant. Under a recently developed unified scheme for non-native species impacts, *P. annua* can be considered a species that can cause potentially moderate to major impacts in Antarctica. If current patterns of increased human pressure and regional climate change persist and mitigation action is not taken (i.e. reduction of propagule

pressure and eradication or control measures), *P. annua* is likely to spread in Antarctica, especially in the Antarctic Peninsula region, with significant negative consequences for some of the most remote and pristine ecosystems worldwide. Tighter biosecurity across all operators in the region, improved surveillance for the species, and prompt, effective control actions will reduce these risks.

Keywords

Invasions, *Poa annua*, Climate change, Competition, Antarctic ecosystems

Introduction

Biological invasions represent significant conservation challenges. A focus on their early stages, such as the pathways of, and barriers to, invasion is valuable given a cost-efficacy continuum exists from prevention, through early detection and rapid response, to eradication (Simberloff et al. 2013). The latter is usually the most costly management option and may have unanticipated consequences (Zavaleta et al. 2001). Such efforts are predicated on the assumption many invasive non-native species either have or will have substantial impacts (Catford et al. 2012; Richardson and Ricciardi 2013). However, recent reviews have argued that our understanding of impacts often remains poor, and: (1) a more substantive evidence base is required to improve management of non-native species given criticisms that impacts are unproven or cannot be predicted (Hulme et al. 2013); (2) despite considerable advances in understanding the early stages of the invasion pathway, forecasts of the conditions under which substantial impacts will be realized remain weak (Ricciardi et al. 2013); (3) generalizations regarding the groups most likely to cause impact, the suites of traits associated with impact, and the environments most sensitive to impacts, remain uncommon (Pyšek et al. 2012).

A consistent theme across these reviews is that predictions of impact are needed because impact is often used to assess the need for early intervention, and specifically which species or groups of species, and under what conditions, should be the subject of such intervention. Much uncertainty remains, however, about the species that will have most impact and the conditions under which such impact will be realized (McGeoch et al. 2010; Ricciardi et al. 2013). Although data mining approaches and meta-analyses are beginning to reduce this uncertainty (Vilà et al. 2011; Greenslade and Convey 2012; Pyšek et al. 2012), further quantification and forecasts of impacts are essential to improve management efficacy and reduce the impacts of biological invasions (Simberloff et al. 2013; Richardson and Ricciardi 2013). Although these priorities apply to invasions generally, they are particularly significant in the context of the conservation challenges faced by protected areas. Understanding the correlates or determinants of non-native species richness variation can assist with managing risk in the early stages of the invasion process (Wilson et al. 2009; Foxcroft et al. 2011). However, for management decision-making about eradication or control, either after initial detection or later in the invasion process, understanding the potential for negative effects on the ecophysiological performance of native species and the community functioning is essential.

Antarctica (including the sub-Antarctic islands) is considered to include many examples of the world's last remaining wilderness areas (Convey and Lebouvier 2009; Shaw et al. 2014). The continent itself is protected under the Protocol on Environmental Protection to the Antarctic Treaty (Tin et al. 2009), and parts of most of the surrounding sub-Antarctic islands are either formally protected under national legislation, have World Heritage status, or both (Chown et al. 2001; de Villiers et al. 2005). Biological invasions (along with climate change and interactions among these two change drivers) are the most significant terrestrial conservation challenges facing the region (Frenot et al. 2005; Chown et al. 2015a; Hughes et al. 2015). In consequence, an increasing amount is known about the correlates of invasion, the pathways for and vectors of non-native species, and the management strategies required to limit inadvertent introductions, especially given deliberate introductions are, for the most part, not permitted to the continent and its surrounding islands (Hughes and Convey 2012; Molina-Montenegro et al. 2014; McGeoch et al. 2015; Hughes and Pertierra 2016). Nonetheless, as is more broadly the case, the extent of information on impacts is surprisingly limited, particularly for plants (Gremmen et al. 1998; Frenot et al. 2001; Le Roux et al. 2013; Molina-Montenegro et al. 2012a), which is remarkable given that plants together with invertebrates are the most speciose groups of non-native species across the region (Frenot et al. 2005; Hughes et al. 2015), and are showing propensity for establishment on the continent itself (Molina-Montenegro et al. 2014). In consequence, the evidence base for decisions about management actions to be taken for either established species or new arrivals is currently small (Hughes and Convey 2012). Nevertheless, some efforts have been conducted to eradicate non-native plants from Antarctica (Galera et al. 2017; Pertierra et al. 2017a). For example, *Poa pratensis* was successfully eradicated in January 2015, providing pivotal information about eradication actions, allowing for the generation of a management protocol with high cost-efficacy, likely applicable to another non-native plant species in Antarctica (Pertierra et al. 2017a).

Here we begin to address some aspects about the impacts and management for the most widespread non-native vascular plant species in the Antarctic, *Poa annua*, which currently is the only non-native species of flowering plant that has successfully established a reproducing population on the Antarctic Peninsula (Frenot et al. 2005; Chwedorzewska 2009). This species is commonly associated with anthropogenically-modified habitats worldwide, but currently can also be found as an introduced species in natural habitats on most sub-Antarctic and some maritime Antarctic islands as well as a number of locations on the north-west coast of the Antarctic Peninsula (Molina-Montenegro et al. 2012a; Chwedorzewska et al. 2015; Hughes et al. 2015; Atala et al. 2019), and has been forecast to become more widespread (Chown et al. 2012; Pertierra et al. 2017b). Experimental laboratory studies have shown this species can potentially outcompete the only two flowering plant species indigenous to the Antarctic continent, the grass *Deschampsia antarctica* and the pearlwort *Colobanthus quitensis* (Molina-Montenegro et al. 2012a, 2016).

Here, using field 'common garden' experiments on King George Island (South Shetland Islands), we examined interactions between these three plant species with

regard to variation in relative density of each, as density has been identified as an important factor influencing the invasion process, since higher densities enhance the competitive ability of a given species in a community (Lockwood et al. 2005; Arian and Parrott 2006). We also focus on water availability, as it is the primary limiting component in most Antarctic terrestrial ecosystems (Convey et al. 2014), with *D. antarctica* occupying a wider range of habitats compared with *C. quitensis* in the context of the water regime (Torres-Mellado et al. 2011). Furthermore, coastal parts of the Antarctic Peninsula region have experienced increased precipitation over the last century, a pattern which is forecast to continue (Bromwich et al. 2011; Turner et al. 2014; Thomas et al. 2015; Lee et al. 2017). As well as the indicated increase of temperatures for this area, an increase of precipitations is expected, generating higher soil water availability and hence, enhancing the physiological performance of vascular plants (Torres-Diaz et al. 2016). Combining these two elements (relative competitive ability and increased water availability), this study tested the following hypotheses: *i*) the most widespread non-native plant in Antarctica, *P. annua*, will exert a stronger competitive effect than the native vascular plants *C. quitensis* and *D. antarctica*, as assessed by survival and growth, and *ii*) these competitive effects currently are greater at higher relative densities of individuals of *P. annua* and under higher resource availability, as predicted under a simulated future climate change scenario. The ultimate goal was to provide initial predictions of how *P. annua* will affect native plants in both the short and long term, to aid in evidence-based conservation decision making within the region.

Materials and methods

Study site and target species

The common garden component of the study was conducted on the western shore of Admiralty Bay (King George Island, South Shetland Islands) in the vicinity of the Henryk Arctowski Polish Antarctic Station (62°09'S, 58°27'W). Individuals of *P. annua* used to perform this experiment were collected from a single population. Mean annual temperature at this location is -2.8 °C, and mean annual precipitation is 700 mm, falling mainly as snow, but increasingly as rain in summer (Kejna et al. 2013). Soils in this area typically have a high content of coarse mineral particles, high total organic carbon, low C/N ratio, acidic pH, and local enrichment of nutrients due to input by seabirds (Beyer et al. 2000; Androsiuk et al. 2015).

The well-developed vegetation of this area includes communities dominated by *Colobanthus quitensis*, *Deschampsia antarctica*, and many cryptogams (Smith 2003). *D. antarctica* demonstrates wide ecological amplitude and environmental tolerance here, colonizing habitats ranging from mineral to organic soils and from dry to waterlogged areas (Bravo et al. 2009). *C. quitensis*, although often reported as co-occurring with *D. antarctica* (Convey 1996), is less tolerant to extreme conditions, preferring moist

soils (Smith 2003). *P. annua*, is conspicuous in the area, occurring in plant communities with the two native flowering plants (Fig. 1), and as a pioneer in glacial forelands (Olech and Chwedorzewska 2011). *P. annua* was recorded for the first time in the Antarctic in 1953 on Deception Island, South Shetland Islands (Chwedorzewska et al. 2015). In the austral summer of 1985/1986, some individuals were observed for the first time adjacent to the Polish Antarctic Station Henryk Arctowski (Olech 1996). Subsequently, increases in density within the original area, and spread into new areas dominated by native vegetation, were documented. More recently, the development of flowers and production of fertile seeds in the majority of individuals of *P. annua* in this area has been recorded (Wódkiewicz et al. 2013) as well as the formation of a viable seed bank (Wódkiewicz et al. 2014). During the austral summers of 2007/2008 and 2009/2010 individuals of *P. annua* were found further south in new localities on the northern Antarctic Peninsula (Molina-Montenegro et al. 2012a). According to available genetic and historical data, it appears *P. annua* was introduced with soil from Poland, imported for use in the station greenhouse in late 1970s. Nonetheless, high levels of genetic variation in the Antarctic population at King George Island suggest multiple introductions from different sources may have taken place (Chwedorzewska and Bednarek 2012), a likely scenario given the species is widespread in many cold environments (Frenot et al. 2005; Pertierra et al. 2017b).

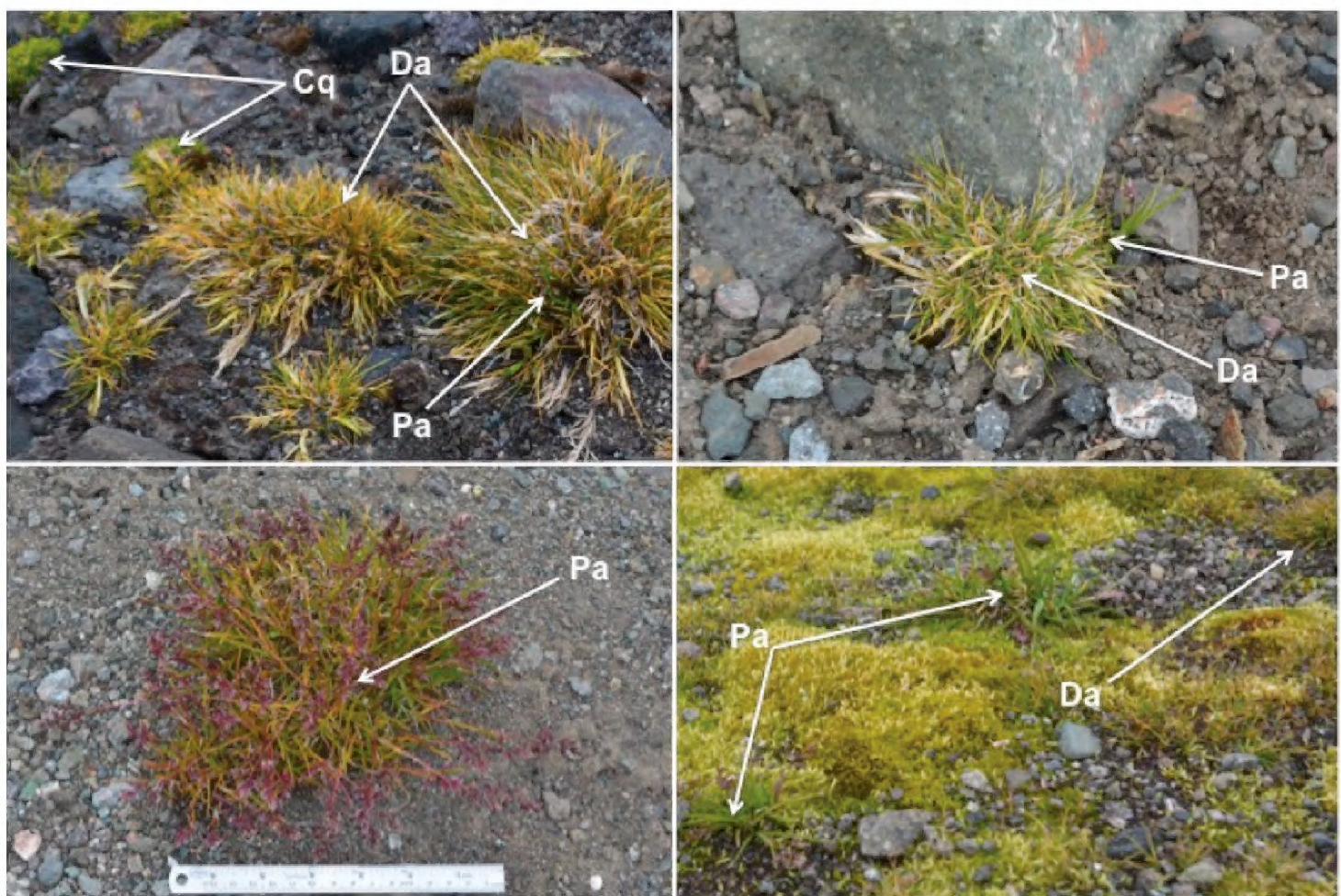


Figure 1. *Poa annua* (Pa) individuals occurring in plant communities with the two native vascular plants *Colobanthus quitensis* (Cq) and *Deschampsia antarctica* (Da), both in the vicinity of the Henryk Arctowski Station and on the pioneer zones on glacial forelands.

Field experiments

Manipulative field transplant experiments were established to assess the effects of *P. annua* on growth and survival of *C. quitensis* and *D. antarctica*, as well as the competitive interactions among the native species, using plant density and soil water as independent variables. Thus the elements within these common garden trials were three species and four density challenges under two climate states (current and predicted future).

Individual adult healthy plants/tussocks (6–7 cm height) of all three species were collected randomly in the vicinity of Arctowski station in January 2011. Each plant/tussock was carefully uprooted with soil around its roots (ca. 100 g) and maintained well-watered in a plastic box under natural light and temperature ($1420 \pm 120 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $3.7 \pm 0.8 \text{ }^{\circ}\text{C}$) conditions for a maximum of 2 h until transplanted. Plant status was visually assessed just before the next step in the transplant procedure to ensure undamaged individuals were used (plants showing foliar and/or root damage were excluded). These common garden trials were established above the shoreline, where they were exposed to seawater aerosols, and fertilized by water rich in nutrients flowing down from a nearby penguin rookery. The natural vegetation of this site includes dense continuous patches of *D. antarctica* as well as *C. quitensis*, mosses and lichens (Chwedorzewska et al. 2008). Nevertheless, this trial was carried out in a patch without cover vegetation in order to avoid modifying the competition intensity, as well as availability of resources in the soil.

The two-way density challenge consisted of the ‘focal species *vs.* the ‘competitor’ species at four relative plant densities (i.e. 4 density treatments) in an experimental unit (0.25 m^2) with each of the three species being both the target or competitor species in the experimental design (see Fig. 2). High relative density consisted of 10 individuals of the focal species *vs.* five individuals of the competitor species. Medium relative density consisted of seven individuals of the focal species *vs.* eight individuals of the competitor species. Low relative density consisted of five individuals of the focal species *vs.* 10 individuals of the competitor species. Finally, 15 individuals of each species (*P. annua*, *C. quitensis* and *D. antarctica*) in monoculture were planted without the presence of another species, as controls. Individuals were planted at least 5 cm apart. Each density treatment was replicated five times across the total transplant plot of 2500 m^2 ($50 \times 50 \text{ m}$) and two plots were constructed, one for the current and the other for the future climate scenario. The future climatic scenario focused on our calculation of future water availability.

Water regime was examined for both current conditions and a simulation of projected conditions for the region within the next 100 years, which involves an increase in soil water availability of ca. 20–25% (IPCC 2013; Turner et al. 2014). Current conditions were assessed by sampling soil moisture in the study site early in the growing season (January 2010). Using a tensiometer (2725 Series Jet Fill, CO, USA), matric water potential of the soil at 5–7 cm depth at 10 points in the study site was measured. Points were randomly selected and separated by 2–3 m. Soil moisture recorded in the field was -29 ± 0.51 (Mean \pm SE) kPa. Based on these data, a matric water potential

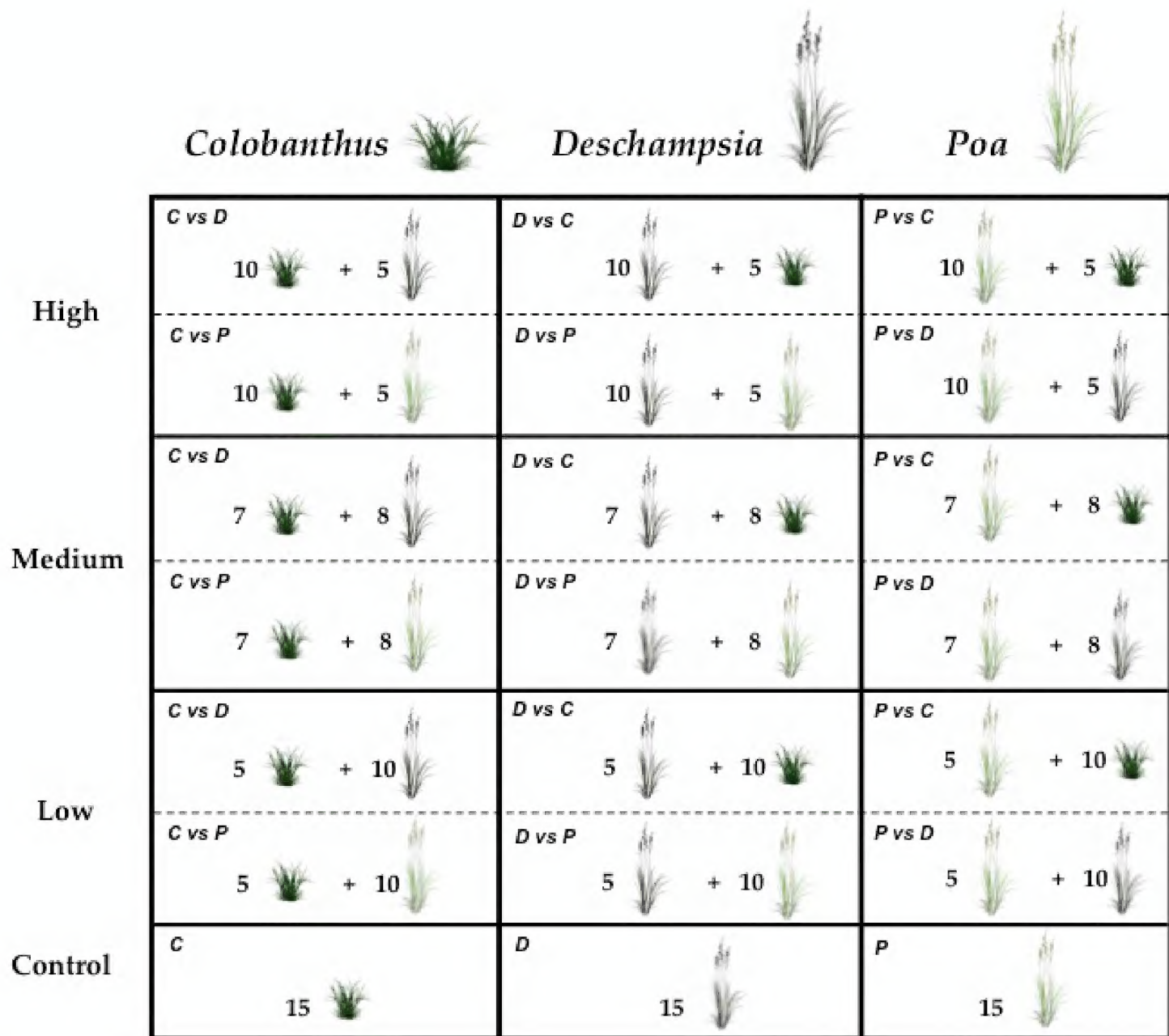


Figure 2. A schematic of the design of the common garden experiment, illustrating all combinations of competitive interactions performed between the three study species (*Deschampsia antarctica*, *Colobanthus quitensis* and *Poa annua*) at high, medium and low relative density, as well as the controls (monocultures). This design was replicated five times in the field for both current and future climate scenarios.

of -20 kPa was estimated for the future scenario. A pilot trial in the field was then undertaken to determine the volume of water to be added to individuals transplanted into the field situation to attain this soil moisture level (-20 kPa). This required an extra 120 ml of water per week. Thus, two treatments were applied to each experimental unit: current conditions (no manipulation) and future climate condition (weekly water addition) to sampling plots for the entire period of the experiment (2 months). Matric water potential was measured five times over the duration of the experiment to verify that differences between treatments were maintained (mean values recorded for current and future climate condition: -29.4 ± 3.7 and -19.2 ± 2.1 , respectively).

Every plant collected in the study area was randomly assigned to one of the experimental plots and measured prior to the start of experimental treatments. The plants' height was measured using a digital caliper (Mitutoyo; resolution: 0.01 mm) and initial wet weight was measured using a digital balance (Boeco BPS 52 plus; resolution:

0.01 g). Before recording the biomass, the soil was carefully removed, avoiding damage to the roots in order to record only the vegetation tissue. A two-way ANOVA showed no differences in initial height among individuals of each species that were assigned to the different treatments and no differences in wet weights for those individuals of *C. quitensis* assigned to different treatments ($F_{3,16} = 0.34$; $p = 0.79$ and $F_{1,16} = 1.47$; $p = 0.24$, respectively), and likewise for *D. antarctica* ($F_{3,16} = 0.27$; $p = 0.84$ and $F_{1,16} = 1.69$; $p = 0.21$, respectively), and for *P. annua* ($F_{3,16} = 0.54$; $p = 0.66$ and $F_{1,16} = 0.41$; $p = 0.53$, respectively).

Transplants were carried out during the 2010–2011 growing season and fresh biomass and survival were evaluated over 8 weeks. Survival percentage both in native and non-native species was evaluated *in situ* every two weeks and estimated by means of the Kaplan-Meier method, and statistical differences were assessed with Cox-Mantel test (Fox 1993). At the end of the experiment, all individuals that survived were removed from the site, weighed to obtain final dry mass (dried for 48 h at 60 °C and weighed) and then incinerated. Each plot site was rehabilitated by smoothing disturbed soil to match the surrounding surface pavement as closely as could be achieved without causing further disturbance.

The final biomass and survival values were compared using analyses of variance (ANOVA). Initially, all data were compared to investigate differences in the main factors of species, relative density and climatic scenario (current conditions and simulated future wetter conditions). Then, a two-way ANOVA was used to assess total biomass and survival at the end of the experiment. All analyses were conducted separately for the current conditions and the future scenario, considering the species (*P. annua*, *C. quitensis* or *D. antarctica*), relative densities (low, medium, high or control) and treatment (growing in monoculture, with a native or with a invasive species) as main factors. For all the ANOVAs, the assumptions of normality and homogeneity of variances were evaluated using Shapiro-Wilks and Bartlett tests, respectively (Sokal and Rohlf 1997). All analyses were performed with Statistica 6.0.

Results

Field experiments

Overall, mean plant biomass at the end of the experiment did not differ for any of the three species, *C. quitensis*, *D. antarctica* or *P. annua*, under current climate conditions compared with the wetting scenario ($F_{1,72} = 3.96$ $p < 0.23$, $F_{1,72} = 2.12$ $p < 0.43$ and $F_{1,72} = 1.98$ $p < 0.46$, respectively). Similarly, mean survival did not differ between climate scenarios in any of the species ($F_{1,72} = 2.06$ $p < 0.44$, $F_{1,72} = 2.01$ $p < 0.51$ and $F_{1,72} = 3.18$ $p < 0.11$, respectively). Nevertheless, several interactions were significant, indicating that under wetting conditions the invasive *P. annua* could exert a stronger competitive effect on both native species.

Evaluation of survival patterns over time

Under current water conditions, survival percentage of *C. quitensis* at high relative densities (i.e. 15 plants in monoculture or 10 individuals of *C. quitensis* and 5 individuals of other species) was significantly higher in monoculture or high density than when growing with the invasive *P. annua* (Cox-Mantel test = 10.21; $p = 0.031$), but not different when growing with the native *D. antarctica* (Cox-Mantel test = 0.23, $p = 0.97$). The survival percentage of *C. quitensis* in low relative density declined significantly when growing with *D. antarctica* or with *P. annua* (Cox-Mantel test = 12.74, $p = 0.004$ and 17.86, $p < 0.001$, respectively). Although survival percentage of *C. quitensis* decreased significantly when grown with *P. annua*, this trend was more evident at higher relative density, with ca. 50% mortality in the first two weeks. High mortality was not evident in other transplants in such a short time frame. On the other hand, survival in *D. antarctica* at high relative density decreased significantly only when grown with the invasive *P. annua* (Cox-Mantel test = 8.60, $p = 0.033$). At a low relative density of *D. antarctica*, survival percentage decreased significantly when grown with *C. quitensis* or with *P. annua* (Cox-Mantel test = 12.48, $p = 0.021$ and 16.46, $p < 0.001$, respectively) compared with the monoculture treatment. At low relative density of *D. antarctica*, 50% mortality was realized at six weeks when grown with *P. annua*. Finally, *P. annua* showed no differences in survival when growing at high relative density with either *C. quitensis* or *D. antarctica* (Cox-Mantel test = 3.30, $p = 0.12$ and 2.82, $p = 0.33$, respectively). However, when *P. annua* was grown at a low relative density its survival also declined significantly (ca. 50%) in the presence of *D. antarctica* (Cox-Mantel test = 5.24, $p = 0.039$), but non-significantly in the presence of *C. quitensis* (Cox-Mantel test = 2.21, $p = 0.069$).

Under the future, less water-limited scenario, *C. quitensis* at high relative density showed significant mortality when growing with *P. annua* (Cox-Mantel test = 6.80, $p = 0.034$), but not when growing with *D. antarctica* (Cox-Mantel test = 0.12, $p = 0.93$). Similarly, *C. quitensis* at low relative density showed a sharp decrease in survival over time when growing with *D. antarctica* or with *P. annua* (Cox-Mantel test = 6.54, $p = 0.038$ and 8.76, $p < 0.001$, respectively). *C. quitensis* showed an abrupt decrease during the first week (ca. 60% mortality) when growing with *P. annua*. On the other hand, *D. antarctica* at high relative density showed a smooth but non-significant decrease in survival over time when grown in association with either *C. quitensis* or *P. annua* (Cox-Mantel test = 3.72, $p = 0.072$ and 4.68, $p = 0.055$, respectively). At low relative density the survival of *D. antarctica* was significantly lowered when growing with *C. quitensis* or *P. annua* (Cox-Mantel test = 6.31 $p = 0.038$ and 12.92 $p < 0.001$, respectively). Finally, *P. annua* at high relative density showed similar survival curves over time both in monoculture and when growing with *D. antarctica* or *C. quitensis* (Cox-Mantel test = 2.11 $p = 0.089$ and 1.99 $p = 0.11$, respectively). However, at low relative density, *P. annua* survival declined significantly when growing with *C. quitensis* or with *D. antarctica* (Cox-Mantel test = 15.71 $p < 0.001$ and 11.18 $p = 0.034$, respectively), but only when growing with *C. quitensis* was a sharp decrease in survival, of over 50% at four weeks, found.

Evaluation of biomass and survival at end of field experiments

Under current water conditions, the final survival percentage of both native plant species significantly decreased with increase of the relative density of competitors, this being more evident when grown in presence of the invasive *P. annua* (Fig. 3; Table 1). In addition, survival percentage of *P. annua* was significantly decreased only at higher relative density of competitors, in this case being more evident when grown in the presence of *D. antarctica* (Fig. 3; Table 1). Similarly, under the simulated wetting scenario, survival of *D. antarctica* and *C. quitensis* decreased significantly when grown together with *P. annua* compared to the monoculture treatment (Table 1), with a greater effect apparent at higher relative density of competitors (Fig. 3). In addition, the survival of *P. annua* was significantly higher when grown in the presence of either of the native species *D. antarctica* and *C. quitensis*, compared with those individuals growing in monoculture (Fig. 3; Table 1).

Table 1. Results of factorial ANOVA evaluating the interactive effect of species (target species in monoculture or in association with other species) and density (high, medium and low) on biomass and survival in *Colobanthus quitensis*, *Deschampsia antarctica* and *Poa annua*. ANOVAs were conducted independently for each climate scenario. Abbreviations: d.f. = degrees of freedom; MS = mean squared error; F = F-statistic; *P* = *P*-value. Significant *P*-values (< 0.05) are highlighted in bold.

	Current scenario				Wetting scenario			
Biomass	d.f.	MS	F	<i>p</i>	d.f.	MS	F	<i>p</i>
<i>Colobanthus quitensis</i>								
Species	2, 36	8.8	24.8	<0.01	2, 36	22.8	42.9	<0.001
Density	2, 36	2.4	6.8	0.032	2, 36	6.7	12.2	<0.001
S x D	4, 36	1.2	3.3	0.021	4, 36	2.1	3.9	<0.01
<i>Deschampsia antarctica</i>								
Species	2, 36	28.9	68.6	<0.001	2, 36	54.5	181.6	<0.001
Density	2, 36	7.1	14.2	0.220	2, 36	2.3	5.2	0.039
S x D	4, 36	2.5	5.3	0.251	4, 36	1.8	4.4	0.029
<i>Poa annua</i>								
Species	2, 36	5.5	27.4	<0.01	2, 36	2.9	6.9	<0.01
Density	2, 36	0.6	3.1	0.06	2, 36	1.9	4.8	0.017
S x D	4, 36	0.2	1.1	0.36	4, 36	0.5	1.3	0.289
Survival	d.f.	MS	F	<i>p</i>	d.f.	MS	F	<i>p</i>
<i>Colobanthus quitensis</i>								
Species	2, 36	4466.1	1999.7	<0.001	2, 36	6948.6	1200.3	<0.001
Density	2, 36	1011.1	452.7	<0.01	2, 36	1767.3	305.3	<0.01
S x D	4, 36	392.4	175.7	<0.01	4, 36	695.8	120.2	<0.001
<i>Deschampsia antarctica</i>								
Species	2, 36	5789.6	400.5	<0.001	2, 36	9208.6	1235.1	<0.001
Density	2, 36	697.4	48.2	<0.01	2, 36	2068.9	277.5	<0.001
S x D	4, 36	232.7	16.1	<0.001	4, 36	1083.3	145.3	<0.001
<i>Poa annua</i>								
Species	2, 36	1948.8	295.3	0.008	2, 36	2250.8	354.7	<0.001
Density	2, 36	2296.1	347.9	0.012	2, 36	1877.2	295.9	0.022
S x D	4, 36	698.1	105.7	0.018	4, 36	315.6	43.3	0.043

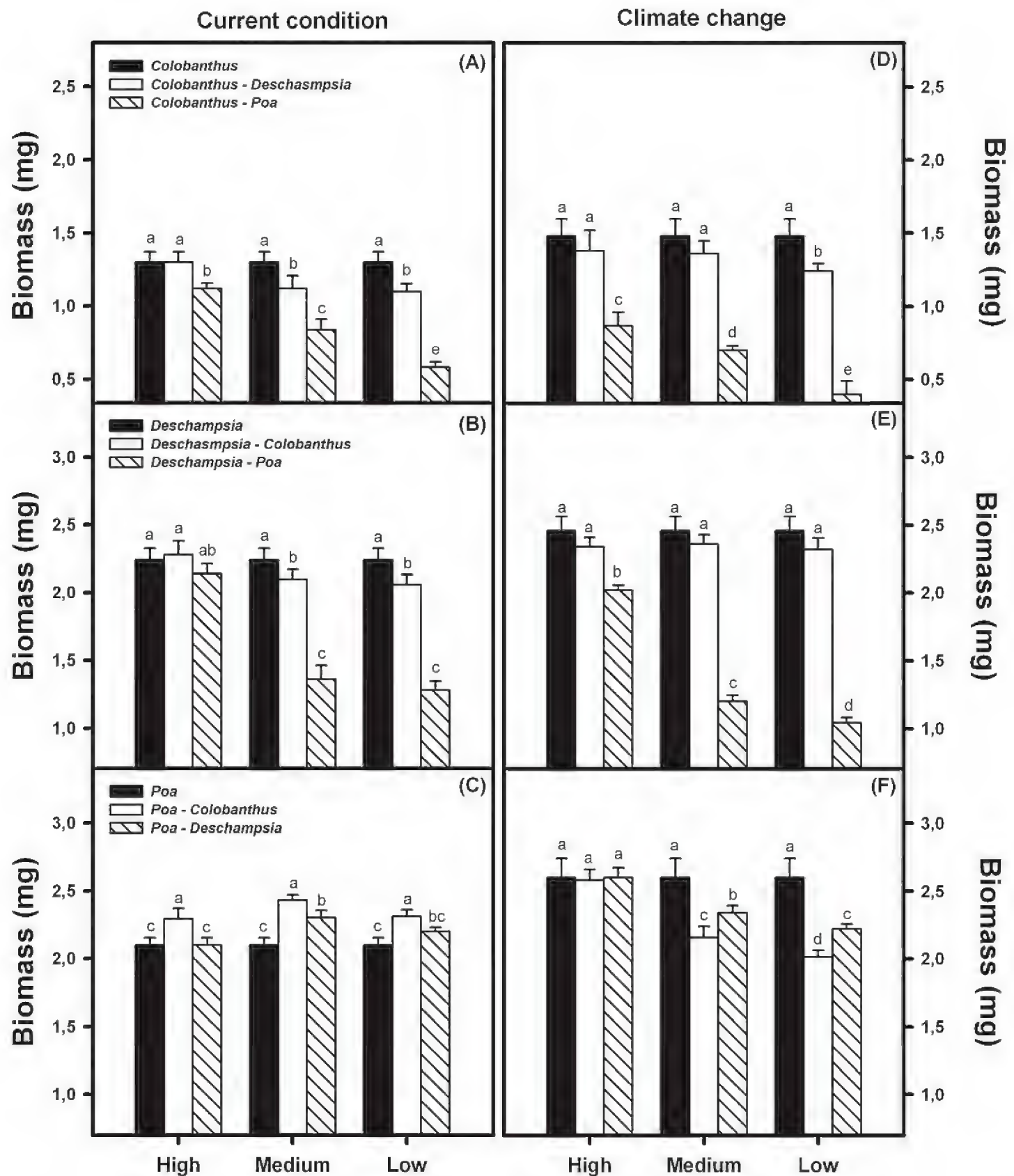


Figure 3. Survival percentages (mean \pm 1 SD) for target species controls (15 plant monoculture – solid bars) compared with survival under different relative densities of competitor species (low, medium and high) for *C. quitensis*, *D. antarctica* and *P. annua* are shown in both a current scenario (**A–C**), and a wetting scenario (**D–F**). Different letters indicate significant differences.

Final biomass in both native species was significantly lower when grown in the presence of *P. annua*, particularly at higher relative density of the invasive species (Fig. 4, Table 1). Conversely, the final biomass of *P. annua* was not affected by increase in the relative density of competitors (Table 1), and significantly increased when grown with *D. antarctica* or *C. quitensis* compared with the monoculture condition (Fig. 4).

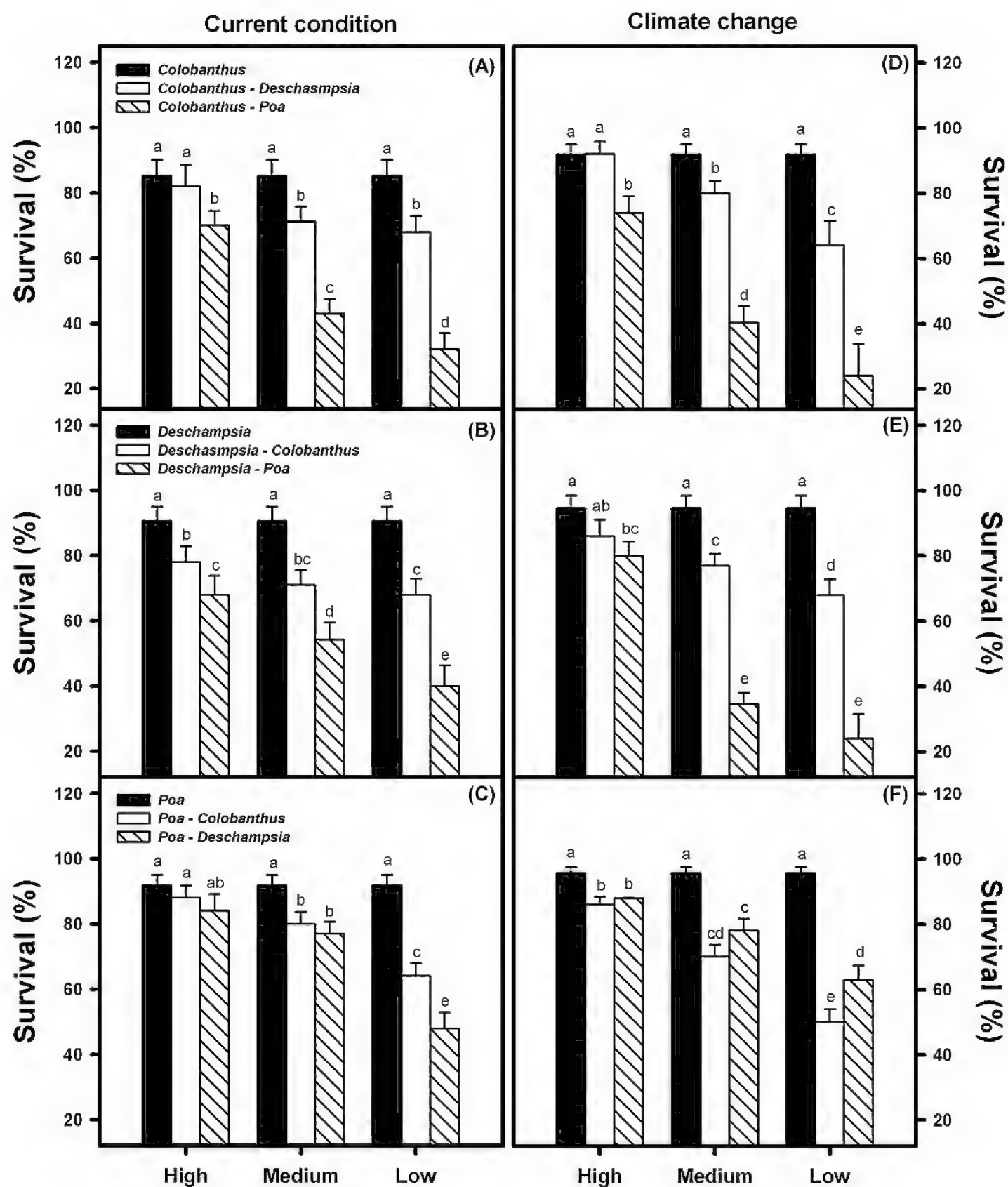


Figure 4. Final individual plant biomass (mean \pm 1 SD) for target species controls (15 plant monoculture – solid bars) compared with biomass under different relative densities of competitors (high, medium, low) for *C. quitensis*, *D. antarctica* and *P. annua* are shown in both a current scenario (A–C), and a wetting scenario (D–F). Different letters indicate significant differences.

Under the wetting scenario, the negative effect of *P. annua* on biomass was greater for *D. antarctica* than *C. quitensis*, and more evident with increase in the relative density of competitors (Fig. 4; Table 1). However, the biomass of *P. annua* significantly decreased with the increase in the relative density of competitors (Table 1), this being more evident when grown with *C. quitensis* than *D. antarctica* (Fig. 4).

Discussion

The combined outcomes of this field study demonstrate explicitly the negative potential impacts of an invasive plant on the native Antarctic vascular flora, and can inform models of how invasion scenarios are likely to play out given current and predicted future climatic conditions. Previous investigations have identified a range of Antarctic areas most susceptible to colonization (Chown et al. 2012; Perterra et al. 2017b) and several of these areas are already being colonized (Olech and Chwedorzewska 2011; Molina-Montenegro et al. 2012a; Hughes et al. 2015). This study advances current understanding by seeking to identify impacts in the field, providing evidence for the relative density required and climatic conditions it may take for a non-native species to invade and then to displace its native competitors.

The marked asymmetry of competitive effects identified, based on the field experiment with *P. annua* and the two native species, suggests that the future spread of *P. annua* may result in the local displacement of both native species. In addition, the data and analyses indicate that knowledge of the relative local frequency dependence of performance between species in competition is important when evaluating the potential for invasion of non-native species in Antarctica. Although *P. annua* performed better than *C. quitensis* or *D. antarctica* at all densities of competitors tested, in general, even low densities of *P. annua* individuals would be sufficient to outcompete and invade the local vegetated areas, both under current climatic conditions and the future, wetter, scenario examined. In addition, other key aspects of potential for invasion, as propagule pressure should be assessed (Colautti et al. 2006; Simberloff 2009), under the specific conditions found at King George Island, in order to know the potential impacts of *P. annua* on the community structure and functioning. Habitats on this island are representative of much of the maritime Antarctic. In the context of the large numbers of propagules estimated to be entering the Antarctic annually (> 70 000 – Chown et al. 2012), including those of *P. annua* and other species that are pre-adapted to the environmental conditions of the region, this finding is of particular concern.

Based on the observation that *P. annua* currently grows associated with other plant species as well as on bare ground on King George Island, we also demonstrate that the probability of invasion depends on an interaction between the native plant species and the specific wetter climate scenario. Thus, invasion of *P. annua* in any new area will depend on whether the area is currently dominated by *C. quitensis* or *D. antarctica*. Under current climate conditions the competitive effect of *P. annua* on *C. quitensis* is greater than on *D. antarctica*. This may be due to *D. antarctica* having a set of functional traits that enables higher performance than *C. quitensis* (see Smith 2003), or because invaders that are functionally dissimilar from native species are often favored (see Richardson and Pyšek 2006; Mayfield and Levine 2010; Gallien et al. 2015). However, under a future scenario of higher soil moisture availability, *P. annua* exerted a weaker competitive effect on *C. quitensis* than on *D. antarctica*. This switching in the competitive effect exerted by the invasive *P. annua* on native species appears to be the result of an increase in the competitive ability of *C. quitensis* under moister conditions.

Alternatively, there may also be an increase in niche overlap of *P. annua* and *D. antarctica* (*sensu* Hutchinson 1957).

Numerous studies have shown relationships between competitive effects and phylogenetic or functional structure in plant communities (Kraft and Ackerly 2010; Kunstler et al. 2012). These studies are based on the assumption that ecological similarity tends to lead to more intense resource competition than ecological dissimilarity (Kunstler et al. 2012). Ecological similarity can be quantified by using functional traits on the basis that these traits are linked to competitive ability such as rapid resource acquisition or biotic tolerance (see Chave et al. 2009). Nevertheless, it has been suggested that processes other than phylogenetic or trait similarity could drive competition between plants, generating a hierarchy in the competitive ability of species (Chesson 2000; Mayfield and Levine 2010). Our results suggest that the hypothesis of phylogenetic or trait similarity must be qualified as a generalized driver of competitive outcomes among Antarctic plants, because the competitive effect induced by *P. annua* on native plants was altered under different abiotic conditions. Previous studies have shown that *P. annua* exerts higher competitive effects on *D. antarctica* under two simulated climate change scenarios (well-watered condition or higher nutrient availability) compared with current climate conditions, due to higher resource use efficiency (Molina-Montenegro et al. 2016). In addition, it has been shown that *C. quitensis* possesses high phenotypic plasticity, improving its resource acquisition and ecophysiological performance under well-watered soil conditions (Molina-Montenegro et al. 2012b). On the other hand, Casanova-Katny and Cavieres (2012) showed that *D. antarctica* performs better when grown in moister microhabitats such as those provided by mosses compared with those in the bare ground, suggesting that this vascular species can be negatively affected in its physiological performance and growth when faced with low water availability. Thus, we suggest that competitive ability in these Antarctic plant communities could be governed by hierarchical differences driven primarily by climate conditions and secondarily by phylogenetic similarity. Such outcomes would also be in keeping with studies illustrating the importance of abiotic conditions altering the outcome of competitive interactions (see Keddy 1989). Although these hypotheses cannot be differentiated in the current study, further field experiments can be designed to unravel the mechanisms' underlying interactions between *P. annua* and native plants under current and future climate scenarios.

There are indications that the well-documented trend of rapid regional warming in the Antarctic Peninsula region over the second half of the Twentieth Century has temporarily ceased (Turner et al. 2016). However, it is clear that over the last several decades the patterns of precipitation and temperature have changed in this region of Antarctica, along with nutrient input to the soil (Vaughan et al. 2003; Convey et al. 2009; IPCC 2013; Turner et al. 2014), with significant impacts on plant populations and communities (Parnikoza et al. 2009; Cannone et al. 2016, 2017). In a complex global change scenario, with simultaneous variation in different factors such as nutrients, temperature and water availability (see also Convey et al. 2014), formerly excluded areas may become available for colonization by those species with higher capacity to

acquire the resources or improve performance, such as many invasive species (Dawson et al. 2012). Scenarios which then include the complexities of community interactions (Grime 2006), including native and alien species with varying functional similarity, in the context of the abiotic variation suggest that the trajectory of influence will differ over time, as the hierarchy of competitive ability is altered, and more complex communities potentially facilitate colonization (Bruno et al. 2003). Thus, studies such as that described here provide the basis for further investigation of how invasive plant species respond to multiple changing abiotic factors in a natural setting in Antarctica. In so doing, the work will also extend understanding of how impacts are realized more generally (see discussion in Catford et al. 2012; Richardson and Ricciardi 2013), and contribute to understanding of the role of ecological similarity in determining competitive outcomes in the context of invasion success, especially under changing climates (Chown et al. 2015b; Gallien et al. 2015; Hulme 2016).

Conservation implications

Overall, this study indicates that the substantial concerns already expressed about invasive plant species for the Antarctic continent (Shaw et al. 2014; Hughes et al. 2015) are warranted, and particularly so for *P. annua* which is already spreading in the region (Olech and Chwedorzewska 2011; Molina-Montenegro et al. 2012a, 2014; Hughes et al. 2015; Atala et al. 2019). Moreover, it provides additional evidence supporting general concerns about the impacts of grasses (Pyšek et al. 2012), and for a region where few investigations have been made of the impacts of invasive alien species on local populations (McGeoch et al. 2015).

These findings underpin the growing number of biosecurity actions in the region and the importance of adherence to mitigation recommendations in the Antarctic Treaty's Non-Native Species Manual (CEP 2011). Clearly, interventions at an early stage in the invasion pathway will be most efficient and cost effective (Simberloff et al. 2013), but substantial investment in their implementation is only likely if it can be demonstrated that negative effects will ensue from colonization by non-indigenous species (Hulme et al. 2013; Ricciardi et al. 2013). This study shows that, without such interventions, impacts will not only take place, but are also likely to change as water availability changes in the future along the Antarctic Peninsula. Indeed, *P. annua* is clearly a competitor with moderate (MO) to major impact (MR), or at least potentially so for the continent, as defined under the recently developed unified classification for alien species based on the magnitude of their environmental impacts (Blackburn et al. 2014). Such species cause local population decline (MO) or extinction (MR) of at least one native species, and in the case of MR species lead to changes in the structure of communities and the abiotic or biotic composition of ecosystems. In consequence, much impetus exists to improve biosecurity for the region, especially given that its implementation is currently inconsistent among different operators in Antarctica, with improvements required from many operators (Braun et al. 2001; Hughes and Pertierra 2016).

Nonetheless, the impact of *P. annua* is being realized on a continent that is considered a natural reserve, and one of the planet's last wilderness areas and one with expanding ice-free areas (Shaw et al. 2014; Lee et al. 2017). Recent reports confirming that the species has colonized areas away from stations and is expanding along the Antarctic Peninsula are concerning (Olech and Chwedorzewska 2011; Molina-Montenegro et al. 2012a, 2014; Atala et al. 2019). Given that spread can be relatively fast (see Wilson et al. 2007), and we have demonstrated here that *P. annua* is capable of negatively impacting Antarctica's two native vascular species, we encourage the development of a program of eradication that also will enable an effective evidence-based conservation decision-making protocol to be developed and applied in the region.

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